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RESEARCH ARTICLE

Woody semi-natural habitats modulate the effects of field size and functional crop diversity on farmland birds

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Abstract

1. Agricultural intensification has simplified landscape composition and configuration, which has led to biodiversity declines. Increasing landscape-wide crop heterogeneity can promote farmland biodiversity. However, knowledge is still lacking on how the effects of configurational and compositional crop heterogeneity (i.e. field size and crop diversity) are modulated by the amount of semi-natural habitats in the landscape, especially across large scales.
2. We tested how mean field size and functional crop diversity affect farmland bird diversity and abundance over three consecutive years, and how these effects are modulated by the amount of small woody features (SWF) in the landscape. We related data from a national bird monitoring scheme to field-level information from a novel, high-resolution remote sensing-based crop type map.
3. Smaller field sizes and higher functional crop diversity were not generally associated with a higher diversity or abundance of farmland birds. Associations varied with species' breeding habitat preferences and were modulated by the amount of SWF.
4. In landscapes with a low SWF amount, species diversity and the abundance of species breeding in field edges or shrubs were negatively associated with increasing field size. However, where the amount of SWF was high, larger field size was associated with higher species diversity and abundance of field and shrub breeders. Diversity increased with higher functional crop diversity, as did the abundance of non-field breeders in landscapes with a medium to high SWF amount. Field size tended to have a stronger effect on bird diversity and abundance than functional crop diversity.

5. *Policy implications*: National and EU agricultural policies should adopt a landscape perspective by considering the amount of semi-natural habitats when designing biodiversity-enhancing measures that target field size and functional crop diversity. In landscapes with low SWF amount, decreasing field sizes may be particularly effective to promote farmland bird diversity and the abundance of non-field breeders. In landscapes with a medium to high SWF amount, increasing functional crop diversity is likely more effective than reducing field sizes. Field and shrub breeders may be promoted by maintaining landscapes with large fields, only if these offer a high SWF amount, low agronomic yield potential and low productivity.

KEYWORDS
agricultural intensification, biodiversity conservation, Common Agricultural Policy, farmland biodiversity, landscape heterogeneity, monitoring, small woody features

1 | INTRODUCTION

The expansion and intensification of agriculture are major drivers of biodiversity loss (Díaz & Malhi, 2022). As a large proportion of the world's surface is shaped by agriculture, biodiversity conservation in human-dominated agricultural landscapes is of crucial importance (Tscharntke et al., 2005). Given the ongoing decline of farmland biodiversity (Rigal et al., 2023), there is an urgent need to redesign agricultural landscapes.

Across Europe, land management and landscape structure have been changing for centuries. Since the 1950s, changes were mainly due to agricultural intensification, industrialisation and abandonment (Jepsen et al., 2015). Crop rotations and crop portfolios became less diverse (Martin, Cadotte, et al., 2019a), while the size of management units increased (Jepsen et al., 2015), leading to an increasing homogenisation of the landscape (Clough et al., 2020). The configuration of landscapes (size, shape and spatial arrangement of land-use patches) and their composition (varying proportion and heterogeneity of land-use types) are key determinants of biodiversity patterns and associated ecosystem services (Dunning et al., 1992; Fahrig et al., 2011).

More heterogeneous landscapes allow for a greater variety of organisms and species to coexist, accompanied by greater resource diversity across the life cycle due to complementation and niche differentiation effects (Benton et al., 2003; Dunning et al., 1992; Fahrig et al., 2011). In simplified agricultural landscapes, attempts to restore landscape heterogeneity by increasing the amount of semi-natural habitat (e.g. species-rich grassland and woody features) affect biodiversity positively (Tschumi et al., 2020; Vallé et al., 2023). However, given the strong competition for land on productive soils, increasing the amount of semi-natural habitats by taking agricultural land out of production might be difficult (McKenzie et al., 2013). Therefore, in addition to the protection of the remaining (semi-) natural habitats, increasing crop heterogeneity in terms of configuration (i.e. reducing crop field size) and composition (i.e. diversifying crop types) can make agricultural landscapes more biodiversity-friendly without sacrificing productive land (Sirami et al., 2019; Tscharntke et al., 2021).

Farmland biodiversity benefits from increased configurational crop heterogeneity through decreasing field size (Clough et al., 2020; Fahrig et al., 2015) and increasing field border length (Alignier et al., 2020; Martin, Dainese, et al., 2019b). Decreasing landscape-level field size can have equally strong effects on the multitrophic diversity of farmland biota as increasing the cover of semi-natural habitats (Sirami et al., 2019). Increasing crop diversity is assumed to benefit biodiversity, but results are inconsistent showing positive (Ekroos et al., 2019; Fahrig et al., 2015), negative (Martin et al., 2020) and mixed effects (Hiron et al., 2015; Josefsson et al., 2017; Sirami et al., 2019). The relative contributions of compositional and configurational crop heterogeneity to increase farmland biodiversity have rarely been tested (but see Fahrig et al., 2015; Sirami et al., 2019). However, disentangling these two components is important because it is not yet clear which of these is more effective in promoting biodiversity in agricultural landscapes. Variation in responses to differences in compositional or configurational crop heterogeneity can be species-specific (Miguet et al., 2013; Šálek et al., 2021), but has also been attributed to ecological species traits, for example in birds (Ekroos et al., 2019; Josefsson et al., 2017). Farmland bird specialists, often ground-nesters originating from tree-less steppes (hereafter field breeders), require large, contiguous habitat patches and avoid breeding close to small woody features (hereafter SWF) such as hedgerows and woodlots. Other farmland birds breed within SWF (hereafter shrub breeders), whereas some require open herbaceous vegetation at field edges (hereafter edge breeders) to build their nests and use SWF as requisites (e.g. song posts or for cover).

The amount of SWF varies regionally and constitutes 'semi-natural' habitats or features of cultural landscapes that increase landscape complexity. As species' breeding habitat preferences may drive responses to landscape heterogeneity (Hiron et al., 2015; Pickett & Siriwardena, 2011), the effects of compositional and configurational crop heterogeneity on species abundance and diversity might be modulated by the amount of SWF (Bretagnolle et al., 2019; Sirami et al., 2019). Field breeders, for example, may benefit from smaller fields because of the higher availability of food resources in field borders (Thomas & Marshall, 1999). Yet, if SWF amount is high, they might prefer larger fields as they can keep a certain distance to SWF and avoid the associated predation risk (Laux et al., 2022). For more details on potential mechanisms of how SWF could modulate the effects of crop heterogeneity on the bird abundance of species groups, see Text S1 in Supporting Information. Therefore, considering the amount of SWF when separating the effects of compositional and configurational heterogeneity on biodiversity in agricultural landscapes is important to support the efficient design of landscape-scale, agri-environmental policies. Potential interactions between SWF amount and crop heterogeneity have rarely been considered (but see e.g. Ekroos et al., 2019; Sirami et al., 2019). Previous studies aiming at disentangling the effects of crop configuration and composition were often conducted at small spatial scales and used data collected only at local or regional levels or at few study sites from a single year. As crop rotation may cause differences in the effects of crop heterogeneity between years, these might have remained undetected in such studies.

To address these key limitations, we studied the effects of functional crop diversity and mean field size on farmland bird abundance and richness in landscapes with a variable amount of SWF over three consecutive years. We combined a large, national-scale monitoring dataset on common farmland bird abundance and diversity with novel crop type maps from remote sensing to test the following hypotheses:

H1. Farmland bird diversity and abundance decrease with increasing mean field size, because larger fields reduce the access to adjacent fields and edge habitats that provide foraging resources and breeding habitat.

H2. Farmland bird diversity and abundance increase with increasing functional crop diversity, because a higher diversity of functional crop types creates foraging and breeding niches for more species, benefits species with complex habitat requirements and insures against the temporal loss of habitat types during important life cycle periods.

Beyond these directional hypotheses, we tested whether the amount of SWF modulates the responses of bird diversity and abundance to mean field size and functional crop diversity. We expected that predation risk and the availability of foraging and nesting sites shift along a gradient of SWF amount and depending on species' breeding habitat preferences.

2 | MATERIALS AND METHODS

2.1 | Bird data

We used data on bird occurrence and abundance for the years 2017–2019 from the Common Breeding Bird Survey (CBBS) of Germany (Kamp et al., 2021), which is organised regionally and coordinated by the DDA. In this scheme, volunteers annually map all birds along routes of ca. 3 km length four times between 10 March and 20 June. Routes are situated within quadratic plots of 100 ha (hereafter CBBS plots) that were selected across Germany in a randomly stratified approach (for details, see Kamp et al., 2021). Bird raw data are combined into territories within the boundaries of the CBBS plots using standard territory mapping methods at the end of each season. We selected 18 common bird species using farmland as breeding or feeding habitat (Hertzog et al., 2023). We excluded species mainly breeding in buildings or in forests because factors other than those covered in this study might affect their populations. Based on their breeding habitat preferences, we allocated the species to three functional groups: (i) in-field ground breeders (*field breeders*) that avoid SWF in agricultural landscapes; (ii) field-edge ground breeders (*edge breeders*) that preferentially breed at the edges of fields but also use SWF as habitat requisites; and (iii) *shrub breeders* that breed in hedgerows or trees in the agricultural landscape (Figure S1).

We used the number of territories as the abundance value per CBBS plot, year and species group. We calculated the exponent of Shannon's entropy (Hill–Shannon diversity) in package 'vegan' v. 2.5–7 (Oksanen et al., 2020) as a value of species diversity, as it accounts for differences in abundance between species without overemphasising common or rare species:

$$^{1}D = \exp\left(- \sum_{i=1}^{s} p_i \ln(p_i) \right), \quad (1)$$

where p_i is the proportion of species i and s is the number of species (Hill, 1973).

We constrained our analysis to CBBS plots that contained at least 30% agricultural land (arable and grassland) based on national land-use maps (GeoBasis-DE/BKG, 2015).

2.2 | Land cover data and landscape metrics

We used Sentinel- and Landsat-based crop type maps of Germany (years 2017–2019, 24 crop types, 10 m resolution) from Blickensdörfer et al. (2022) to calculate compositional and configurational crop heterogeneity. We calculated both metrics for each CBBS plot and year to provide landscape-level characteristics that are ecologically relevant to birds and several other taxa (Sirami et al., 2019). We used R 4.1.3 (R Core Team, 2022) for spatial data processing with package 'sf' v.1.0–7 (Pebesma, 2018).

Previous studies have used the area of a contiguous patch of the same crop as a measure of field size (Noack et al., 2022). However, several fields of the same crop in direct vicinity might appear as a single field, and field borders that act as important refuges for farmland birds might be missed (Figure S2A). We aimed to approximate realistic management units (Figure S2B) by applying the multiresolution segmentation algorithm (Baatz & Schäpe, 2000) in the eCognition software (Trimble Germany GmbH, 2019) to a time series of monthly Sentinel-1 and Sentinel-2 composites (Tetteh et al., 2021). We interpreted segments as individual fields and calculated arithmetic mean field size as a measure of configurational crop heterogeneity based on all segments intersecting a CBBS plot (for details, see Text S2).

We used Hill–Shannon diversity of crop types (including grassland) as a measure of compositional crop heterogeneity analogous to the bird diversity measure (Equation 1). A distinction of habitats representing farmland birds' requirements was suggested as an important factor in studies on the effects of landscape heterogeneity on birds (Fahrig et al., 2011; Josefsson et al., 2017). Therefore, rather than treating each crop as a different category (e.g. winter wheat and winter barley), we grouped crops into categories of similar structure, sowing time, height and cover (e.g. winter cereals) and calculated the functional diversity of crop groups (i.e. functional crop heterogeneity; Table S1).

We calculated the amount of SWF (trees, hedgerows and woodlots) in hectares based on data from Blickensdörfer et al. (2022). We observed annual differences in SWF between the three study years. This was unexpected, as there are high legal obstacles in Germany to clear-fell small woody features and to remove hedgerows. Hence, classification accuracy likely varied across years; SWF gains or losses were rather artefacts than actual changes. To account for differences in the amount of SWF per CBBS plot between years, we retained only those pixels that were classified as SWF in at least 2 out of the 3 years (for details, see Text S3). Our approach resulted in a final set of 842 CBBS plots used for analysis (Figure S3). Spatial patterns of all variables can be found in Figures S4–S6.

2.3 | Statistical analysis

We modelled bird diversity and abundance as a function of mean field size and functional crop diversity using Bayesian generalised linear mixed effects models. We fitted all models in R 4.1.3 (R Core Team, 2022) using package 'brms' v2.16 (Bürkner, 2017) with weakly informative priors (Table S2). We fitted models for all 3 years separately, as we were interested in the temporal robustness of the results.

To assess whether the amount of SWF in agricultural landscapes modulates the effects of crop heterogeneity on farmland birds, we fitted interactions between field size and SWF amount, as well as functional crop diversity and SWF amount. We added total farmland area and grassland area per CBBS plot as covariates to account for differences in habitat availability. We included an interaction of the two variables, as available farmland area might drive farmland bird abundance and diversity differently in arable versus grassland-dominated landscapes. All predictor variables were scaled and centred prior to analysis. Correlations between variables were always below Pearson's $r = |0.4|$ (Table S3).

We stratified our sample by soil climate regions (Roßberg et al., 2007) and allowed intercepts to vary with region. Thereby, we aimed to account for regional variability in the abundance and diversity of farmland birds as a result of varying pedo-climatic conditions that potentially also reflect differences in agricultural production. We used a truncated Gaussian (TN) error structure to model species diversity with truncation values of 0.9, as Hill–Shannon diversity does not reach values below 1. Models fitted to species diversity data followed the form:

$$y_{ij} \sim TN\left(\mu_{ij}, \sigma_{\text{species diversity}}\right)$$

where y is species diversity modelled as an outcome of a TN distribution with an expected value μ and a standard deviation σ. Index i refers to the individual plot and j to the soil climate region. Expected values were modelled as follows:

$$\begin{aligned}\mu_{ij} = \beta_{0j} &+ \beta_1(\text{field size}_i) + \beta_2(\text{functional crop diversity}_i)\\ &+ \beta_3(SWF_i) + \beta_4(\text{field size}_i \times \text{SWF}_i)\\ &+ \beta_5(\text{functional crop diversity}_i \text{x SWF}_i)\\ &+ \beta_6(\text{farmland}_i) + \beta_7(\text{grassland}_i)\\ &+ \beta_8(\text{farmland}_i\ x \text{ grassland}_i)\end{aligned}$$

We further summed the number of territories per CBBS plot, species group and year to estimate the effects of crop heterogeneity on the abundance of species with similar breeding habitat preferences (field, edge and shrub breeders). We fitted abundance models per species group with a negative binomial (NB) error structure. Abundance models for edge and shrub breeders followed the form:

$$y_{ij} \sim NB\left(\mu_{ij}, \sigma_{\text{abundance}}\right)$$

where y corresponds to the abundance modelled as an outcome of a NB distribution with an expected value μ and a deviation parameter σ.

Expected counts were modelled as follows:

$$\begin{aligned}\log(\mu_{ij}) = \beta_{0j} &+ \beta_1(\text{field size}_i) + \beta_2(\text{functional crop diversity}_i)\\ &+ \beta_3(\text{SWF}_i) + \beta_4(\text{field size}_i \times \text{SWF}_i)\\ &+ \beta_5(\text{functional crop diversity}_i \text{x } SWF_i)\\ &+ \beta_6(\text{farmland}_i) + \beta_7(\text{grassland}_i)\\ &+ \beta_8(\text{farmland}_i\ x \text{ grassland}_i)\end{aligned}$$

A zero-inflation term θ was added to the model of the abundance of field breeders, as we observed zero inflation (ZI) in this dataset. This model followed the form:

$$y_{ij} \sim \text{ZINB}\left(\mu_{ij}, \sigma_{\text{abundance}}, \theta_i\right)$$

where y corresponds to the abundance modelled as an outcome of a zero-inflated negative binomial distribution with an expected value μ and a deviation parameters σ and θ. Expected counts were modelled in the same way as for the NB models and the coefficient θ as:

$$\text{logit}(\theta_i) = \alpha_0 + \alpha_1(\text{farmland cover}_i) + \alpha_2(\text{SWF}_i)$$

For all models, we allowed intercepts to vary between soil climate regions. Intercepts varying between regions were modelled as an outcome of a normal distribution (*N*) as follows:

$$\beta_{0j} \sim N(0, \sigma_{region})$$

We used default sampling settings but ran four chains with 4000 iterations each, half of which were used as burn-in and discarded. To assess model fit, we compared the cumulative density of observed abundances with 50 samples derived from the model using the function 'pp_check' from package 'brms', ensuring that all model parameters showed Rhat values below 1.1 and an effective number of samples larger than 400 (Vehtari, 2021). We used the package 'DHARMa' v4.5 (Hartig, 2019) for posterior model checks based on simulated scaled residuals. We tested for residual spatial autocorrelation using Moran's I and inspected spatial correlograms using functions implemented in package 'ncf' v1.2–9 (Bjørnstad & Falck, 2001). Goodness-of-fit was assessed with conditional and marginal R^2 (function 'bayes_R2'). We also considered unimodal responses of field size and functional crop diversity and estimated the difference in predictive performance between models using a linear and a hump-shaped relationship with function 'loo_compare' from package 'brms'. We calculated the posterior probability of the effect of field size being larger than the effect of functional crop diversity to assess which variable had a stronger impact on the diversity and abundance of farmland birds with the function 'hypothesis' from package 'brms'.

We extracted posterior draws of mean field size, functional crop diversity and their interactions with the amount of SWF. We computed the conditional effects of mean field size and functional crop diversity along an SWF gradient comprising 95% of the observed values, ranging from 0.2 to 20 ha. We derived model predictions of functional crop diversity and mean field size for a low (1 ha), medium (5 ha) and high (13 ha) amount of SWF, representing the 10%, 50% and 90% quantiles of the data. Farmland and grassland areas were kept constant at their mean.

3 | RESULTS

All model parameters were sampled efficiently (effective sample size >400) and converged (Rhat < 1.1). A comparison of models with linear versus quadratic effects of mean field size and functional crop diversity showed similar or higher predictive accuracy for linear models (Table S4). We thus only present results of the more parsimonious linear models. Posterior predictive checks suggested that predicted values were similar to observed data (Figure S7) and there was no spatial autocorrelation in the scaled model residuals (Figures S8 and S9). Generally, the effects of mean field size, functional crop diversity and their interactions with the amount of SWF on the different responses were of similar magnitude and showed similar effect directions in at least 2 out of 3 years (Figure 1). We hence present predictions of species groups' abundance and species diversity only for the year 2018 (Figure 2), but show predictions for all 3 years in Figures S10–S13.

3.1 | Field size

There was no evidence for a consistent negative effect of increasing mean field size on species diversity or abundance per species group (Figure 1a). Field breeders' abundance was even higher where fields were large. Edge breeders' abundance and species diversity tended to decrease with increasing mean field size. We therefore reject H1. The effect of mean field size on diversity and abundance varied with the amount of SWF in at least 2 years (Figure 1b).

The negative effects of increasing mean field size were highly probable (95% CrI) in landscapes with SWF below two to four hectares (Figure 3a). Yet, edge breeders' abundance and species diversity were negatively associated (80% CrI) with larger fields up to 6 ha of SWF, representing approximately 50% of the examined CBBS plots (median: 5 ha). Where SWF amount was larger than ca. 3 ha, field breeders' abundance was positively associated with larger fields in all 3 years (Figure 3a). With an increasing amount of SWF, a positive effect of mean field size on shrub breeders and species diversity became more likely. In landscapes with SWF amount above ca. 12 ha, shrub breeders' abundance and species diversity increased in at least 2 years with high probability.

3.2 | Functional crop diversity

Higher functional crop diversity was associated with higher farmland bird diversity and abundance of shrub breeders, but not necessarily of field and edge breeders (Figure 1c). There was no clear response in field breeders' abundance to higher crop diversity along the SWF gradient (Figures 2b and 3b), giving only partial support to H2. In contrast, the effects of functional crop diversity on species diversity and shrub and edge breeders increased with the amount of SWF (Figure 1d), and positive effects were highly probable for medium to high amount of SWF (>4–6 ha) (Figure 3b).

3.3 | Comparing effects of field size and functional crop diversity

There was large variation in the responses to increases in mean field size and functional crop diversity between species groups (Figures 2 and 3), but the magnitude was often larger for mean field size, especially in landscapes with high or low SWF amount (Figure 4).

3.4 | Joint effects of field size and functional crop diversity along the SWF gradient

In landscapes with a low amount of SWF, edge and shrub breeders' abundance decreased with increasing mean field size, as did species diversity. Only field breeders remained unaffected by changes in mean field size (Figure 2a).

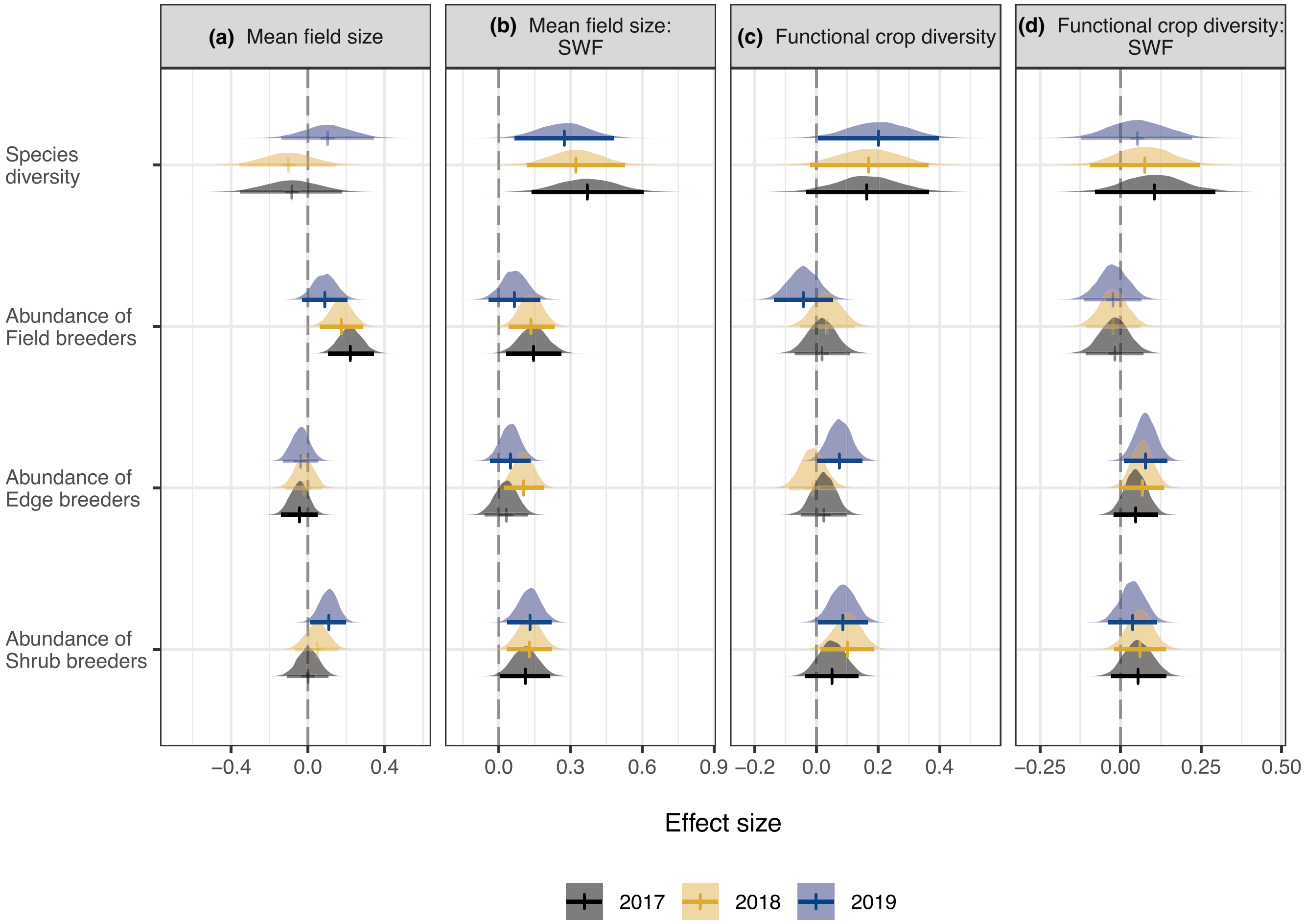

FIGURE 1 Effects of field size (a), interaction between field size and small woody features (SWF) (b), functional crop diversity (c) and its interaction with SWF (d) on farmland bird diversity and abundance of field, edge and shrub breeders per year. Density, mean and 95% credible intervals (CrI) of posterior distributions of effect sizes are given. Credible intervals are printed bold if the probability of an effect reached values of over 80%.

There was no clear effect of functional crop diversity on any response variable in landscapes with low SWF amount. With medium SWF amount, the magnitude of functional crop diversity or mean field size effects was similar, except for field breeders (Figure 4). In such landscapes, an increase in functional crop diversity was associated with higher species diversity and abundance of shrub breeders, but an increase in mean field size was negatively associated with edge breeders' abundance and species diversity (Figures 2 and 3). Only field breeders' abundance increased with increasing mean field size in landscapes with medium SWF amount.

Where SWF amount was high, landscapes with a larger mean field size were associated with higher field and shrub breeders' abundance and tended to harbour higher species diversity. Effects on edge breeders varied between years if SWF amount was high (Figure S11). In such landscapes, increases in functional crop diversity had a positive effect on non-field breeders and species diversity. Yet, increasing mean field size had a stronger and more positive impact than functional crop diversity on all response variables except for edge breeders in 2018.

4 | DISCUSSION

We found that landscapes with larger fields were not generally associated with a lower diversity or abundance of farmland birds. Similarly, a higher functional crop diversity did not show consistently higher abundance and diversity of farmland birds. Both relationships were largely modulated by the amount of SWF in the landscape and were dependent on species' breeding habitat preferences. It is therefore essential to consider woody semi-natural habitats when assessing the effects of crop heterogeneity on biodiversity in agricultural landscapes.

Landscapes with smaller fields have been shown to be associated with higher abundance (Fahrig et al., 2015; Šálek et al., 2021) and diversity (Ekroos et al., 2019; Noack et al., 2022) of farmland birds, within-field plant diversity (Alignier et al., 2020), arthropod abundance (Martin, Cadotte, et al., 2019a) and multitrophic diversity across regions (Sirami et al., 2019). Our results support earlier findings that the effect of decreasing field size varies with the cover of semi-natural habitat (Martin, Cadotte, et al., 2019a; Sirami

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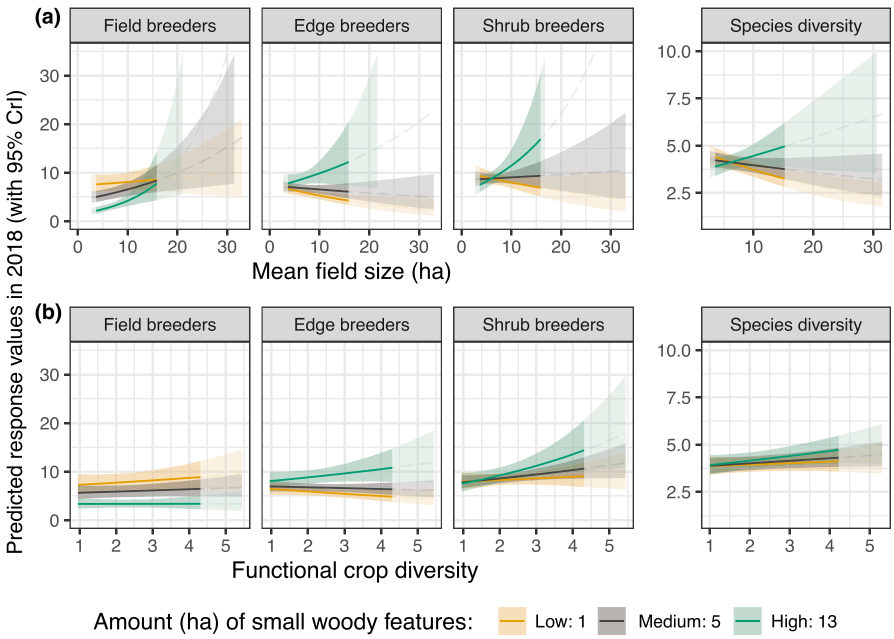

FIGURE 2 Predicted farmland bird abundance of field, edge and shrub breeders and diversity along gradients of (a) mean field size and (b) functional crop diversity for 2018. The amount of small woody features was categorised into three classes based on the 90% (i.e. high amount), 50% (i.e. medium amount) and 10% (i.e. low amount) quantiles. Predictions are highlighted for the range that contains 95% of the measured predictor values across years. Note different *y*-axis scales.

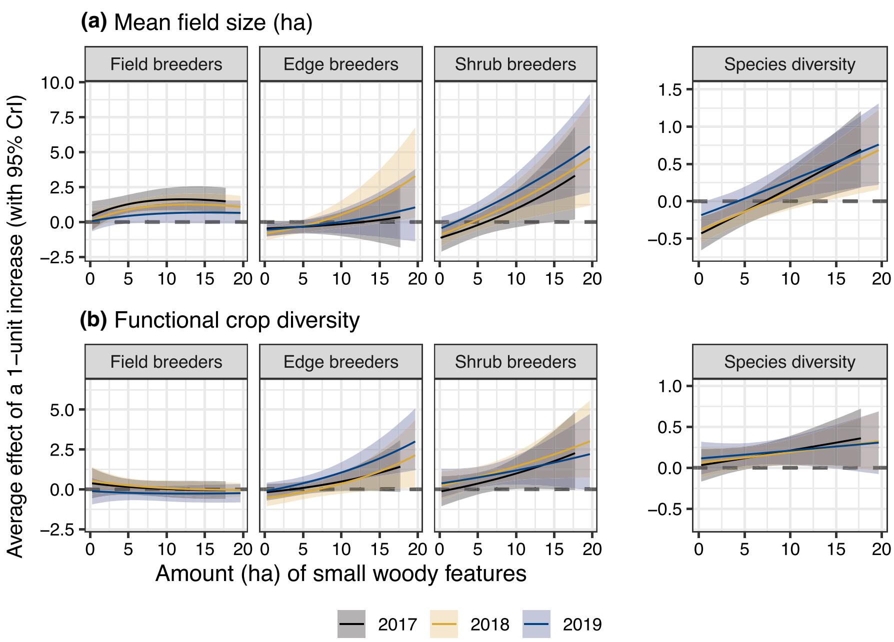

FIGURE 3 Average marginal effects of (a) a 1-ha increase in mean field size and (b) a 1-crop increase in functional crop diversity on bird abundance of field, edge and shrub breeders and farmland bird diversity with 95% credible intervals along a gradient of small woody features for each year. The SWF gradient represents 95% of all observed values. Note different *y*-axis scales.

et al., 2019). We observed higher bird diversity and abundance of edge and shrub breeders with smaller mean field size in landscapes characterised by low to medium SWF amount (<2-6%). Smaller mean field size usually leads to a higher density of margins and higher microhabitat diversity. Especially when semi-natural habitats are scarce, field margins act as refuge foraging or breeding habitat (Vickery et al., 2002). Recent studies, however, found higher within-field plant diversity with smaller field size (Alignier et al., 2020) and higher multitrophic diversity even in the absence of semi-natural vegetation between fields (Sirami et al., 2019). Smaller fields could thus increase seed and arthropod availability, even if vegetation between fields is lacking. Beyond the large, positive effects of landscape-level reductions in field size (Tscharntke et al., 2021), smaller field sizes may negatively affect farm- and field-level economics through a variety of mechanisms, for example increased working time, input costs and lower yields (Clough et al., 2020), but can also facilitate pollination and pest control from field edges, leading to higher yields in arable-dominated landscapes (Martin, Cadotte, et al., 2019a). Consequently, reducing field sizes in arable-dominated landscapes with few SWF might not only increase farmland bird diversity and abundance but potentially could also leverage synergies with agricultural production goals by promoting functional biodiversity and yield-enhancing ecosystem services.

Field breeders (e.g. Eurasian Skylark or Meadow Pipit) remained unaffected by mean field size in landscapes with low SWF amount, and showed higher abundance with larger field sizes in most

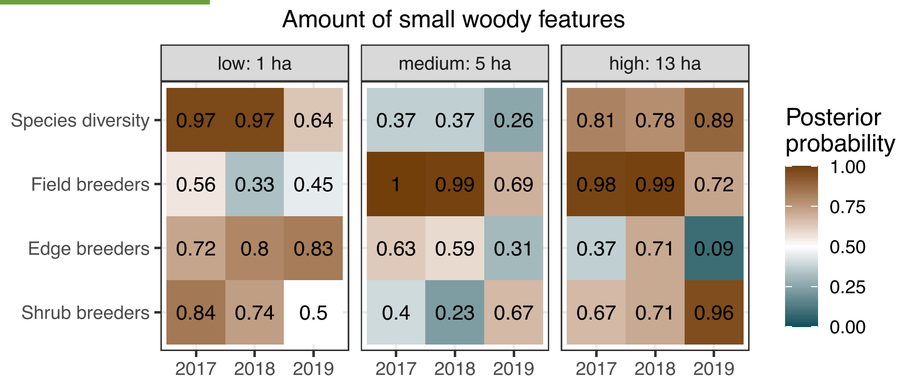

FIGURE 4 Comparison of posterior probabilities of the effects of mean field size and functional crop diversity on farmland bird diversity and the abundance of field, edge and shrub breeders for the 3 years. Numbers represent probabilities of the effect of mean field size being larger than the effect of functional crop diversity for the 10%, 50% and 90% quantiles of the amount of small woody features (SWF). A posterior probability of 0 indicates a stronger effect of functional crop diversity (dark blue) based on the posterior samples, while a value of 1 indicates a stronger effect of mean field size (dark brown).

landscapes, mirroring results from Sweden (Josefsson et al., 2017). Their preference for larger fields is likely explained by an avoidance of SWF (Donald, 2004) that are frequently visited by predators (Laux et al., 2022). Contrarily, field edges do not seem to negatively affect field breeders' abundance in landscapes where SWF are scarce. There, field margins might even provide valuable feeding habitat (Thomas & Marshall, 1999) and lead to increased numbers of field breeders (Guerrero et al., 2012). However, we did not observe higher abundances of field breeders in landscapes with smaller fields, even if SWF amount was low. As we excluded fields smaller than 0.5 ha because of the low accuracies of segmentation results (Tetteh et al., 2021; Text S2), mean field size is likely overestimated, especially in fine-grained landscapes. This might limit the explanatory power of estimated effects for landscapes with small field sizes. In addition, landscapes with low amount of SWF showed a high agronomic yield potential (soil quality rating, Figure S14B). Hence, a higher management intensity might mask the positive effects of smaller fields.

We found no effect of functional crop diversity on field breeders' abundance, irrespective of the amount of SWF. This is surprising, because species breeding within fields can also benefit from habitat complementation during the breeding season (Ekroos et al., 2019; Miguet et al., 2013). Yet, no effects of functional crop diversity on field breeders (Josefsson et al., 2017) or on farmland bird diversity (Redlich et al., 2018) have been shown at landscape scale. Higher functional crop diversity leads to higher resilience and provides an insurance effect due to higher heterogeneity in harvest phenology and therefore resource availability (Benton et al., 2003). Other factors, such as reduced invertebrate availability through pesticide use (Geiger et al., 2010), could potentially overrule this. However, higher functional crop diversity might still contribute to habitat complementation at home-range scale (Pickett & Siriwardena, 2011) and lead to higher nest success of field breeders (Püttmanns et al., 2022).

We found a positive effect of functional crop diversity on non-field breeders, consistent with Josefsson et al. (2017). Yet, the effects of functional crop diversity on abundance and species diversity of farmland birds were negligible in landscapes with low SWF amount, and were positive only at higher amount of SWF. Especially for shrub breeders, breeding habitat availability is likely a limiting factor in landscapes with low SWF amount, perhaps explaining the observed pattern. With higher SWF availability, this limitation should no longer hold, and a positive effect on shrub breeders' abundance and farmland bird diversity is likely the result of greater food availability (Vasseur et al., 2013). Differences in crop management possibly result in more continuous access of and higher resilience in food resources in space and time for farmland birds (Benton et al., 2003; Schellhorn et al., 2015). Similar results indicating a more positive effect in landscapes with high semi-natural vegetation cover have been reported for multitrophic diversity, including birds (Sirami et al., 2019). The interaction of crop diversity with semi-natural vegetation might also explain the large variation in study results on crop diversity effects (Guerrero et al., 2012; Martin et al., 2020; Redlich et al., 2018).

In landscapes with medium to high SWF amount, field breeders' abundance and species diversity increased with field size. This could be explained by large fields providing potential breeding habitat for field breeders, as these can keep a preferred minimum distance from SWF. Contrary to earlier studies, we found a positive effect of larger fields on shrub breeders' abundance in landscapes with high SWF amount. The uncertainty around the estimated effect is high (see credible intervals in Figures 2 and 3), most likely because these landscapes are rare in Germany (ca. 15% of all our study plots). Therefore, these results should be treated with caution, also because model results only explained up to 10% of the variance in shrub breeders' abundance (Table S5).

Our findings of the positive effects of larger fields on shrub breeders' abundance in landscapes with high SWF amount could be due to methodological or ecological reasons. The detection probability of shrub breeders might vary with SWF configuration, but we could not account for this because data of repeat visits were not available. Excluding plots with very large fields (>20 ha) or both high amount of SWF and large fields (SWF > 10 ha & mean field size

>10 ha) did not change our results (Figure S15). Therefore, our findings likely reflect ecological patterns potentially linked to (1) higher within-field vegetation heterogeneity; (2) lower agronomic yield potential and related lower management intensity; and (3) reduced predation risk in landscapes characterised by large fields offering a high SWF amount.

First, large fields situated in landscapes with a high amount of SWF might show high within-field vegetation heterogeneity, caused by uneven plant growth due to environmental and management heterogeneity (Clough et al., 2020). Large fields are mostly found in north-eastern Germany (Figure S14A), where they are dotted with small water bodies of glacial origin (kettle holes) that have not been ameliorated yet and are usually surrounded by SWF (Kalettka & Rudat, 2006). As such within-field heterogeneity can enhance foraging and nesting success for edge and shrub breeders (Vickery & Arlettaz, 2012), they might prefer large fields that include such isolated, high-quality habitats (Batáry et al., 2012). As we assigned crop types to fields based on the dominant crop type (Text S2), we could not consider within-field heterogeneity, perhaps a worthwhile endeavour for future analysis using high-resolution satellite data such as Rapid Eye or Planet Scope (Silveira et al., 2023).

Second, considering only plots with the highest amounts of SWF (>10 ha), we found evidence for lower yield potential (Figure S14B) and lower crop productivity (lower values of the Enhanced Vegetation Index, Figure S16) in plots with large field sizes. Hence, large fields situated in such landscapes might be managed less intensively (e.g. less fertiliser and pesticide applications). Such low-intensity croplands can provide increased structural vegetation diversity and higher food resources for foraging farmland birds, including shrub breeders (Newton, 2004). In contrast, the agronomic conditions for agriculture (i.e. yield potential) are more favourable in landscapes characterised by a high amount of SWF and small fields in Germany (Figure S14B). These conditions could promote a more intensive land use with higher inputs per unit area (Clough et al., 2020; Kapfer, 2007), reflected by higher crop productivity (Figure S16). As a result, the positive effects of small field sizes on shrub breeders' abundance could be compromised. However, available data on the use of agro-chemical inputs (pesticides and fertilisers) are still very coarse (Rigal et al., 2023) which prevented us from testing the influence of land-use intensity on our results.

Third, a higher abundance of shrub breeders could be linked to reduced predation risk in landscapes with large field sizes caused by differences in SWF configuration. Where fields are large, SWF patches are also larger and their density is lower (Figures S14C and S17). For (especially aerial) predators, nests of shrub breeders are more difficult to detect and access in wide hedgerows and larger woodlots (Barkow, 2002). The influence of arboreal mammalian predators may decrease where connectivity between SWF patches and between SWF and forests is low (Ludwig et al., 2012).

Although farmland bird diversity and abundance of field and shrub breeders might benefit from larger fields in areas with high SWF amount, enlarging fields would be detrimental to a variety of other taxa and, as such, to farmland biodiversity overall (Martin, Cadotte, et al., 2019a; Sirami et al., 2019). In such landscapes, although the effects of functional crop diversity were weaker than the effects of mean field size, increasing functional crop diversity not only supports farmland bird diversity and non-field breeders, as we show here, but can also increase the resilience of agricultural landscapes to extreme weather events (Renard et al., 2023) and even lead to higher cereal yields (Smith et al., 2023).

5 | CONCLUSIONS

We show that the responses of farmland bird diversity and abundance to field size and functional crop diversity were largely modulated by the amount of woody semi-natural habitats in the landscape and by species' breeding habitat preferences. Clearly, a landscape perspective is needed to harness the benefits of reductions in field size and increases in functional crop diversity on farmland biodiversity. With respect to the European Union's Common Agricultural Policy, we therefore emphasise that biodiversity conservation measures should be adapted and prioritised to different landscape contexts. To promote bird-friendly agricultural landscapes, policy measures should be tailored to contexts where they will be most effective. Reducing mean field size may be particularly effective to promote bird diversity and the abundance of non-field breeders in landscapes where SWF are scarce. In landscapes with a medium to high amount of SWF, increasing functional crop diversity may be more effective than reducing field sizes. In landscapes offering a high SWF amount, farmland bird diversity and the abundance of field and shrub breeders may even benefit from maintaining larger fields because predation risk is likely reduced and larger fields are characterised by low agronomic yield potential and low productivity. Future studies integrating information on field-level land-use intensity and within-field heterogeneity based on a larger sample in landscapes with a high amount of SWF and a broad range in field sizes are needed to fully understand the effects of crop heterogeneity on farmland birds and possibly other organisms.

AUTHOR CONTRIBUTIONS

Claudia Frank, Johannes Kamp and Sebastian Klimek conceived the idea; Claudia Frank, Johannes Kamp, Lionel Hertzog, Sebastian Klimek, Norbert Röder und Hannah GS Böhner defined the questions and the methodological approach; Claudia Frank, Marcel Schwieder, Gideon Okpoti Tetteh, Christian Levers and Jakob Katzenberger prepared, assembled and provided the data; Claudia Frank carried out analyses and led the writing; Johannes Kamp and Holger Kreft supervised; All authors contributed substantially in the writing process and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest or personal relationships that could have influenced this work.

DATA AVAILABILITY STATEMENT

Code and data to reproduce the analysis and main figures are available via Zenodo at https://doi.org/10.5281/zenodo.10354740 (Frank et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Text S1. Description of potential mechanisms behind modulating effects of small woody features (SWF) on the effects of field size and functional crop diversity on bird abundance of species groups.

Text S2. Detailed description of crop-type map pre-processing and of the segmentation procedure to delineate individual agricultural fields and to calculate measures of mean field size.

Text S3. Calculation of the amount of small woody features (SWF) and discussion of associated data limitations.

Table S1. Summary statistics of landscape variables used in the analysis.

Table S2. Prior distributions of model coefficients.

Table S3. Correlation matrix (Pearson's correlation coefficients) of predictor variables.

Table S4. Pairwise comparisons of predictive accuracy for models with linear and quadratic effects of field size and crop diversity for species diversity and abundance of species groups per year.

Table S5. Conditional and marginal R^2 values for annual models of species diversity and abundance of species groups.

Figure S1. Prevalence for all considered species and years.

Figure S2. Examples of original pixel-based land cover data compared to processed land cover data within a 3 km^2 buffer around bird monitoring sampling plots.

Figure S3. Distribution of the 842 bird monitoring sampling plots used for analysis across Germany.

Figure S4. Map of small woody feature amount, total area farmed and grassland area per sampling plot across Germany.

Figure S5. Map of mean field size per sampling plot and year, for all plots used for analysis.

Figure S6. Map of functional crop diversity per plot and year, for all plots used for analysis.

Figure S7. Results of posterior predictive checks for annual species diversity and abundance models.

Figure S8. Map of residual spatial autocorrelation (Moran's I) of annual species diversity and abundance models.

Figure S9. Correlogram of model residuals for annual species diversity and abundance models.

Figure S10. Predicted abundance of shrub breeders along gradients of mean field size and functional crop diversity for each year and categories of small woody feature amount.

Figure S11. Predicted abundance of edge breeders along gradients of mean field size and functional crop diversity for each year and categories of small woody feature amount.

Figure S12. Predicted abundance of field breeders along gradients of mean field size and functional crop diversity for each year and categories of small woody feature amount.

Figure S13. Predicted species diversity along gradients of mean field size and functional crop diversity for each year and categories of small woody feature amount.

Figure S14. Map of mean field size at sampling plots with high amount of small woody features (SWF). Mean yield potential and mean SWF patch size are given per categories of SWF amount and field size categories (quartiles).

Figure S15. Results of a sensitivity analysis excluding observations with either very large field size (>20 ha) or both a high amount of small woody features (SWF) and large field sizes (SWF > 10 ha & mean field size >10 ha).

Figure S16. Boxplot of mean enhanced vegetation index (EVI) on arable land for all sampling plots for the year 2018. Differences are displayed per field size category quartiles and separately for categories of small woody feature amount.

Figure S17. Correlation matrix (Spearman' rho) of mean field size and three metrics representing configuration and composition of small woody features (SWF) for observations with a high SWF amount (>10 ha).

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